

Larval Dimorphism and Other Characters of *Heterocampa pulverea* (Grote & Robinson) (Lepidoptera: Notodontidae)

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Abstract: A group of sibling larvae of *Heterocampa pulverea* (Grote & Robinson) from Connecticut showed a very distinct dimorphism of color and pattern with no appreciable intergradation. Of 66 larvae reared to maturity 30 were green, 36 were brown. The dimorphism was apparently not linked with rate of development, sex or any discernible adult characteristic. The larvae of both morphs were highly, but differently, cryptic. Possible adaptive advantages of the morphs are discussed. Dorsal thoracic tubercles in the last larval instar, characteristic of this nominal species, are visible as vestiges in the pupa.

On August 1966 a batch of eggs was obtained from a ♀ *Heterocampa pulverea* at Putnam, Windham Co., Connecticut. The larvae from these were reared on *Quercus coccinea*. Ten were given to another Lepidopterist, but 56 were reared to maturity by the writer, emerging 8–26 October 1966, indoors. It was not until the larvae were in the 4th (penultimate) instar that it was realized that a distinct color and pattern dimorphism existed, approximately half being green and half brown. The two groups were then segregated and reared separately. Records of both types in the last two instars were made by color photography.

Table 1 shows the record of the adults that emerged, grouped by larval morph, sex and the dates of emergence. The adults differ from each other in only very minor details, well within the limits of variation of any series from the region. These data show that the morphs, which must be genetically controlled, are not linked with either sex or rate of development.

The larva of this species was first described by French (1880, p. 83) from an Illinois specimen. Packard (1895, p. 249–250 & 282, Pl. 33, fig. 8–8a) reprinted French's description, described a preserved specimen from Massachusetts, and gave 2 small outline drawings copied from figures of Doubleday of a supposed synonym. Packard also refers to an unpublished colored sketch of the larva by Abbot. The French and Packard descriptions are of green larvae with a pattern not unlike the green morph described and figured here, but differing greatly in some respects. Apparently the white dorsal areas characteristic of both the green and the brown morphs of the present paper, and the lateral white areas of the green one, were not present in the French and Packard specimens, since French refers to these areas as "orange" or "purple," and Packard either does not state what their colors were or else refers to them as "reddish." Neither author mentions a brown larva. The Doubleday figures are too small and simple to be of much value.

It is very likely that the larvae of *pulverea* show a considerable amount of variation, predictably much more than would be expected in a sibling group

TABLE 1. Sibling *H. pulverea* grouped by larval morph, sex and date of adult emergence.

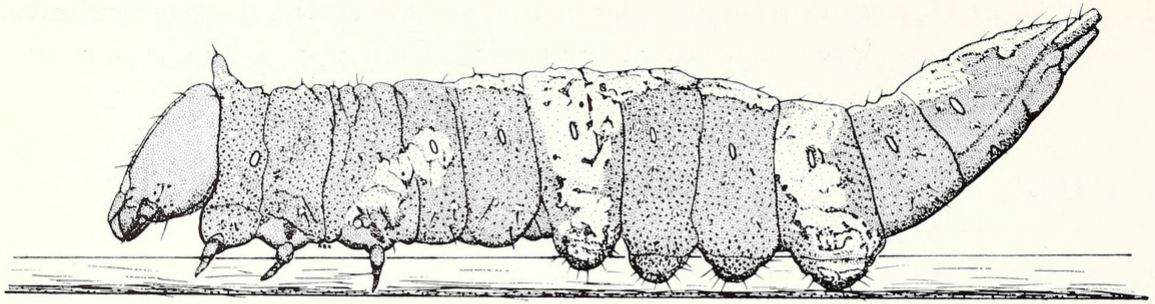
		Green		Brown	
		♂	♀	♂	♀
October	8	2	—	—	—
	9	—	—	—	1
	10	—	3	2	3
	11	2	1	—	—
	12	3	—	1	4
	13	—	—	—	3
	15	2	3	2	3
	16	—	2	—	4
	17	1	1	1	—
	18	—	1	1	1
	19	1	—	4	—
	22	1	—	—	—
	23	—	2	—	—
	26	—	—	—	1
Totals		12	13	11	20

such as that described here. The extent of this in local populations, the amount it is subject to regional variation, and the genetic factors responsible, will all have to be worked out by many rearings of sibling groups and by genetic crosses. At present *H. pulverea* (type locality, Pennsylvania) is considered a northern subspecies of *H. umbrata* Walker (type locality St. John's Bluff, East Florida). It is more than likely that the relationship is a clinal one.

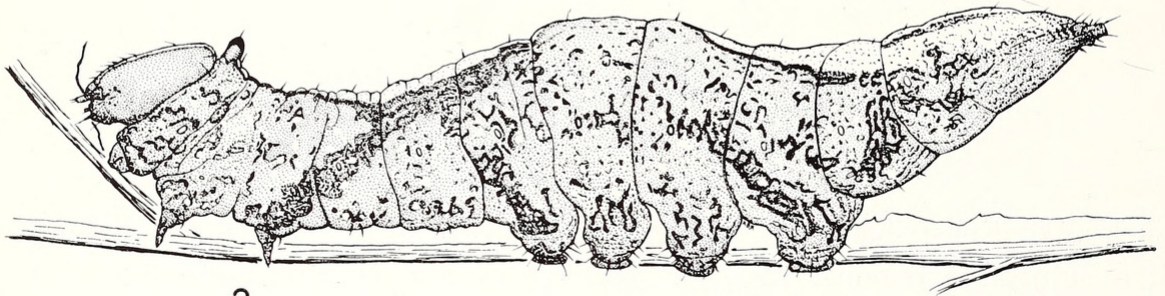
DESCRIPTIONS OF MATURE LARVAE

Green Morph (Fig. 1). Body bright green speckled with small, dark, purplish fuscous dots which remain separate from each other, not coalescing to form lines or scrawls. A distinct white spot around the base of each primary seta. A white patch on either side of metathorax and 1st abdominal segment, running dorso-caudad diagonally from leg base, sometimes barely reaching spiracle, sometimes enclosing it and extending about one or two spiracle's lengths above it. On abdominal segment 3 a broad, white patch running dorsad from the proleg base to join the white dorsal markings, occupying nearly all of the lateral area of the segment. On abdominal segment 6 a similar white patch running dorsad from the proleg base; this may join the white dorsal area or may fail to do so, extending no more than about two spiracle's lengths dorsad of the spiracle. All three of these lateral white patches are very irregularly crenately edged, and contain curved, red-brown dashes and scrawls which differ greatly in extent in different individuals. Rarely there is a small, double patch above each metathoracic leg, and another on the posterior part of abdominal segment 7, largely ventrad of the line of the spiracle.

Dorsally the markings are complex and differ greatly from one individual to another. The fundamental marking is a white dorsal stripe along the entire



1



2

FIGS. 1-2. Mature larvae, *Heterocampa pulverea*, lateral and slightly ventral aspect, drawn from projections of 35 mm. photographs. The setae of both larvae are incompletely shown. Fig. 1, green morph. Fig. 2, brown morph.

length of the body, which is more or less margined and marked internally by dark red-brown scrawls, and differs greatly in width on different segments. Prothorax: stripe unmarked, anteriorly as wide as space between prothoracic tubercles, tapering posteriorly to half as wide, black-edged. Mesothorax and metathorax: stripe narrow anteriorly, widening greatly posteriorly, usually considerably marked internally, and sometimes nearly obliterated, by dark scrawls. Abdomen, segment 1: stripe widening greatly posteriorly to slightly more than half the width of the segment; rarely with any included dark markings, but often pale green mid-dorsally, the green area narrow anteriorly but widening greatly posteriorly so as to leave only narrow, white, tapering edges laterally which in extreme individuals may not reach the posterior edge of the segment. Segment 2: white stripe becoming very broad posteriorly, containing more or less green mid-dorsally. Segment 3: white stripe very broad, laterally confluent with lateral white stripe, from dorsal view occupying all or nearly all of the segment; subdorsally a few small, dark, paired dots and scrawls, especially posteriorly. Segments 4 & 5: white stripe very broad anteriorly, narrowing greatly in segment 4 and still more in segment 5; within it a broad, dark scrawled, X-shaped saddle, centering about anterior edge of segment 5, that may obliterate much of the white. Segments 6 & 7: rarely almost solid green

mid-dorsally with only indications of the white stripe laterally; sometimes with only central portions green, and white stripe on either side of this broad and confluent with lateral white stripe on segment 6. Segments 8, 9 & 10: mid-dorsal area green, white stripe on either side of this broadest at anterior edge of segment 8, narrowing to segment 9, broader at anterior edge of segment 9, narrowing posteriorly; sometimes the green areas of the sides and the mid-dorsal green are confluent along the anterior edge of segment 9, breaking the white stripe.

Brown Morph (Fig. 2). Head, prothoracic tubercles, legs and seta bases as in green morph. Body brown with only a faint greenish cast in recently enclosed individuals. Laterally with no white bands or areas other than a few small areas enclosed by dark scrawls. All brown areas with many irregular, dark brown curved lines and scrawls and smaller, orange-brown dots and curved lines. Dark scrawled markings heavier and coalescing to form a diagonal line running dorso-caudad from base of 3d leg across metathorax and abdominal segment 1 to join dark-scrawled border of dorsal markings. A similar, but less complete, line of markings running dorso-cephalad from base of proleg on abdominal segment 3. A similar, also less complete, diagonal line of dark markings running dorso-cephalad from base of proleg on abdominal segment 6 to spiracle on abdominal segment 5, and more or less continued cephalad across abdominal segment 4. Abdominal segment 7 with dark-scrawled patch caudad and mostly ventrad of spiracle, dorsally more or less joining lateral dark edging of dorsal markings.

Dorsally, fundamental pattern like that of green morph, but with some different distribution of white. Prothorax: as in green morph. Mesothorax & metathorax: also much as in green morph, but with less white, the dorsal areas largely filled in with brown scrawled marks as in the most heavily marked green individuals. A large, irregularly edged, diamond-shaped white area from posterior part of metathorax back to about middle of abdominal segment 4, widest in posterior part of abdominal segment 2; within this for most of its length is a pair of narrow, irregular, closely subdorsal, dark lines. An almost solidly brown saddle (in the same position as the dark-scrawled, X-shaped saddle of the green morph), continuous with brown sides, on posterior half of 4th and anterior half of 5th abdominal segments. A large, posterior white patch, beginning narrowly at about middle of 5th abdominal segment and extending to posterior end; on 8–10th abdominal segments this is more or less filled in dorsally with brown scrawls and lines; within it, as in the anterior white patch, is a pair of irregular, thin, dark, closely subdorsal lines for most of its length.

Despite the considerable amount of individual variation, the two morphs in this group of siblings were very distinct, with no intermediate individuals. The nearest to anything of the sort was in a few larvae of the brown morph that had a greenish tone during the early last instar; and one individual of the

green morph that had the green areas much paler than usual and slightly brownish tinged, but had the green morph pattern.

4TH INSTAR LARVAE

The larvae of this instar are easily recognizable by the ends of the prothoracic tubercles, which have two distinct small, setiferous tubercles at the tips, instead of being terminally smooth as in the 5th instar. On the face these larvae have two thin fuscous lines on either side of the median light area instead of the single line of the 5th instar. The white lateral patches, and to a lesser degree the white dorsal patches, of the green larvae tend to be more obscured by dark scrawls. The brown larvae frequently had considerable of a greenish tinge, although their patterns were definitely of the brown morph.

PRE-PUPAL LARVAE

As the larvae stopped eating and entered the ground for pupation, drastic color changes ensued. All fine details of the pattern disappeared. The brown larvae turned a brilliant pink overall, the dark markings of the saddle on abdominal segments 4 & 5 showing slightly darker. The green larvae, on the other hand, changed to a darker green with the white areas of both the sides and the dorsum very bright pink, making them very conspicuous looking objects. All larvae then became pale and almost colorless just before eclosion to the pupa. The pink larvae that had been brown did this at a uniform rate overall. In the green larvae, however, the pink areas were the first to become colorless, so that for a short time these larvae were green with pale, colorless areas. Doubtless these color changes have some physiological significance, but they can hardly have any protective value (as is the case in some other pre-pupal color changes) since they normally take place underground.

DISCUSSION

The patterns of both of the larval morphs are decidedly, but differently, procryptic, the brown larvae resembling crumpled, dead leaves with shadow or edge patterns, and the green larvae resembling green leaf areas with pieces missing. The larvae of both types are highly disruptive from the dorsal aspect, and the green larvae are disruptive from lateral aspect as well. The white lateral patches are so shaded as to appear almost protuberant and three dimensional. A predator that had learned to recognize the appearance of one of the morphs would be very unlikely, because of this, to react to the appearance of the other one and might very well, in fact, be more likely to ignore the other one if the two were close together. The dimorphism must function in this way as a protective device per se, most valuable when the two morphs are completely different from each other, and still more valuable when each morph is highly cryptic.

The proportions of the morphs in this sibling group and their distinctness from each other strongly suggest a single controlling genetic factor. The evidence of French's and Packard's larval descriptions shows that there is much more larval variation than this sibling group showed, and suggests that the morphs may not always be as distinct from each other. For the time being we suggest that the morphs have evolved, and are maintained, by visual predator selection, but that this may well be strongly affected by all sorts of pleiotropic effects of which nothing is known. Much further work is certainly called for to determine the genetic status, possible pleiotropy and extent within both *H. pulverea* and *H. umbrata* of larval dimorphism.

The pupae all showed vestiges of the prothoracic tubercles. Since these tubercles appear to be present in the 5th instar of only the larvae of *H. pulverea* and *H. umbrata*, their presence in the pupa can be used for identification, at least of *H. pulverea*.

Identification of the material as *H. pulverea* was by comparison with the ♀ type in the American Museum of Natural History. The material here reported upon has been placed in the collection of this museum.

Literature Cited

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PACKARD, A. L. 1895. Mem. Nat. Acad. Sci. **8**: 249-250 & 282, Pl. 33, fig. 8-8a).

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